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POTATO MOSAIC

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BULLETIN 292

POTATO MOSAIC.[1]

DONALD FOLSOM.

SUMMARY

(1) Potato mosaic has been known in Europe for many years and in Maine since 1912. At present it is well established in this state. It is also well distributed over the United States.

(2) The mosaic of tobacco, a plant related to the potato, has been thoroughly studied and apparently is quite similar to potato mosaic. However, there are important differences between the two maladies.

(3) Potato mosaic has certain marked effects upon the appearance, physiology, and yield of potatoes.

(4) It is transmitted by the tubers of infected plants, whether or not these plants have had time to show the usual

[1]This bulletin is largely based upon investigations conducted as a cooperative project between the Office of Cotton, Truck and Forage Crop Disease Investigations of the Bureau of Plant Industry, U. S. Department of Agriculture, and the Department of Plant Pathology of the Maine Agricultural Experiment Station. Such results of this cooperative investigation as are included herewith have already been published in different form as follows: Schultz, E. S., Folsom, D., Hildebrandt, F. M., and Hawkins, L. A. Investigations on the mosaic disease of the Irish potato. Jour. Agr. Research 17:247-274. Pl. A-B (col.), 25-30. 1919. Schultz, E. S. and Folsom, D. Transmission of the mosaic of Irish potatoes. Jour. Agr. Research 19:315-337. Pl. 49-56. 1920. The articles just mentioned are not, however, available to the general reader, except in libraries. Moreover they are written more from the standpoint of the investigator. It is believed that the information contained in them and certain other general information relative to the nature and importance of potato mosaic should be given to the potato growers of Maine as a Station bulletin. Dr. Folsom's name as author of the present publication implies no assumption of credit for work done other than that he has been the Station representative actively engaged in the prosecution of the cooperative investigations on potato mosaic and thus is the logical person to put the results obtained into form for a Station bulletin. Chas. D. Woods, Director.

symptoms before death. This transmission is not modified by seed treatment.

(5) Its infectiousness has been proved by means of grafting and of inoculations with juice from diseased plants.

(6) Aphids, or plant lice, have been shown to be important agents for natural transmission of mosaic from one potato plant to another.

(7) Transmission has been attempted by means of flea beetles, Colorado potato beetles (or "potato bugs"), seed-cutting knives, soil, and contact of seed pieces, leaves, stems, and roots, but has not yet been demonstrated with any of these agents.

(8) The effects of the spread of potato mosaic to healthy plants apparently cannot be avoided by the selection of hills or tubers or by discarding parts of the seed tubers, unless plant lice are controlled.

(9) The relation between this spread and differences between localities, varieties, fertilizers, and spray methods are being studied but have not been fully determined.

(10) Such spread has been reduced by roguing seed plots, that is, by removing mosaic hills as fast as they appear, and absolutely prevented by thorough control of certain kinds of insects.

(11) Potato mosaic is difficult to control but it is now possible to recommend measures that promise to be helpful.

INTRODUCTION.

The disease of Irish potatoes known as mosaic has been known for a long time in Europe, according to Quanjer[2], although without the present name always being applied or the true nature of the disease well understood. It was found to be prevalent in the potato fields of Aroostook County, Maine, in 1912[3]. In 1917 and 1918 it was reported from twenty-one states[4], includ-

[2]Quanjer, H. M. The mosaic disease of the Solanaceae, its relation to the phloem-necrosis, and its effect upon potato culture. Phytopath. 10:35-47. Figs. 1-14. 1920.

[3]Orton, W. A. Potato wilt, leaf-roll, and related diseases. U. S. Dept. Agr. Bul. 64. 48 p. 16 pl. 1914.

[4]U. S. Department of Agriculture. Bureau of Plant Industry. Plant Disease Survey. Plant Disease Bulletin, Vol. [1]-2:1917-1918.

ing all those in which potatoes are an important crop. During 1919 the writer in company with others made a careful estimate of the amount of mosaic in 40 Green Mountain fields in Aroostook County and the same number of Bliss Triumph fields including many which were supposed to be above the average in quality. In these fields the percentage of hills that were mosaic varied from one-half to 100 per cent, averaging 28 per cent for the Mountains and 46 per cent for the Bliss. It is apparent that a mosaic-free field of these two susceptible varieties was extremely rare. As will be shown later, there is every reason to expect that the prevalence of the disease will increase unless effective measures are taken to check it.

Observations upon potato mosaic have been carried on in this country since 1912. Active experimental work has been done in Maine and elsewhere since 1916. Tobacco, a species in the same family of plants as the potato, also has a mosaic disease which has been studied for a number of years and is now comparatively well understood. In spite of all this, progress upon potato mosaic has been slow and it has been only recently that the evidence has justified the formation of definite conclusions regarding it. This delay has been largely due to certain differences of characteristics between tobacco mosaic and potato mosaic[5]. The mosaic of tobacco is far more easily transmitted from plant to plant than that of potatoes. The natural spread of tobacco mosaic is much more apparent than the natural spread of potato mosaic, since the former occurs early in the season while the latter occurs late, or at least the only known agent of potato mosaic transmission in Maine appears in large numbers too late in the short growing season for the newly infected plants to show the disease. Tobacco mosaic is not transmitted from one generation to another through the seeds, but potato mosaic is transmitted by the tubers, so that the full extent and nature of the spread of the latter in the field during any season can be

[5]A more detailed knowledge of these differences can be secured by comparing the two cited papers upon which most of this bulletin is based, with the following.

Allard, H. A. Further studies of the mosaic disease of tobacco. Jour. Agr. Research 10:615-632. Pl. 63. 1917.

Chapman, G. H. Mosaic disease of tobacco. Mass. Agri. Exper. Sta. Bul. 175:73-117. 5 pl. 1917.

ascertained only by growing and examining the progeny of the tubers. While these differences have in the past been puzzling to those who tried to demonstrate similarity between the mosaic of tobacco and that of potato, it now seems that the two are essentially similar maladies and that the principles discovered regarding the former may be safely assumed in general to govern the latter where they have not already been proved to do so, as described in this bulletin. This similarity should now facilitate progress in the study of potato mosaic.

APPEARANCE OF THE DISEASED PLANTS.

The leaves of mosaic potato plants are mottled with light green or yellowish green spots which vary greatly in abundance, location, and shape. They may be merely scattered sparingly, occurring on any part of the leaf, or may be numerous over the whole leaf. They often include or join parts of the larger veins or ribs, but may not come in contact with them. They may appear as dots or circles, but usually are irregular and often are elongate. They may be distinctly set off from the healthy green parts or may fade out gradually. They seldom are more than a quarter of an inch across, altho they may follow a vein for a longer distance. Usually the foliage is wrinkled or ruffled. In fact, this wrinkling ordinarily will be apparent to an observer before the mottling or spotting is, especially if the sunlight is allowed to strike the plants that are being looked at. Diseased plants are frequently dwarfed. Figures 28-30 show diseased leaves and plants.

The preceding description is most characteristic of the disease on the Green Mountain and Bliss Triumph varieties. In some cases with these varieties, and nearly always with Irish Cobblers, the spotting is absent and only extreme dwarfing and wrinkling indicate the presence of the disease. The Rural types seem to display the disease only as dwarfing and leaf wrinkling and curling, if at all. Some other varieties, as indicated later, are as yet not known to have mosaic even when they have been exposed to infection.

The dwarfing and the wrinkling and downward curling of the leaves that may be characteristic of mosaic plants should not lead to confusion with leaf roll, which is characterized by an

FIG. 28. Mosaic potato leaf.

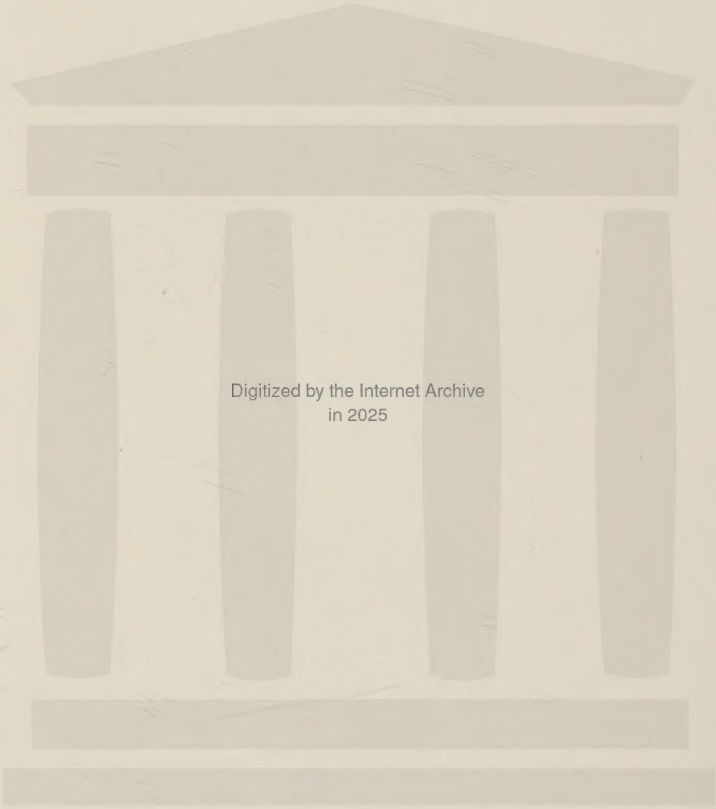

FIG. 29. Mosaic dwarf and healthy Green Mountain hills.

FIG. 30. Mosaic and healthy potato plants produced by tubers from the same lot.

upward rolling of the leaves with dwarfing and a paleness or yellowing not localized in scattered spots. Moreover, this malady, together with certain other inheritable abnormalities of the leaves that may be phases of mosaic, probably requires the same practical treatment as does mosaic.

In a field with many mosaic plants the color of the mass of plants is lighter green, the rows are more ragged, the plants are not so robust or tall, and in case of dry weather yellowing and dying occurs earlier than with healthy stock of the same variety. See Figs. 29 and 30.

Other Effects of the Disease.

A limited number of chemical tests[6] have indicated that mosaic is accompanied by an increase in the amount of sugars in the leaves and by a decrease in the amount of starch. Similar tests may eventually disclose the same differences in the tubers, but at present no way is known for distinguishing healthy dormant tubers from those which are transmitting the disease. The latter germinate as well as the former do. The blossoming stage is reached as soon by diseased plants as by healthy. Vegetative reproduction is modified so that the disease decreases the yield of tubers.

A number of tests have been made by various writers[7] comparing groups of diseased hills with groups of healthy ones regarding the yield of potatoes. These show that the disease in such conditions reduces the yield. They thus agree with the results of similar studies made in Maine, wherein larger numbers of hills were used.

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[6]Schultz, E. S., Folsom, D., Hildebrandt, F. M., and Hawkins, L. A. Op. cit.

[7]Anonymous. Mosaic disease as a factor influencing yield. Potato Magazine 2^5:11, 27. 1919.

Barrus, M. F. Potato-mosaic and certified seed. Potato Magazine 1^4:13-14. 1918.

Murphy, P. A. The mosaic disease of potatoes. Agric. Gaz. Canada 4:345-349. Illus. 1917.

Orton, W. A. Op. cit.

Parker, R. C. Testing seed potatoes on Long Island. Potato Magazine 2^3:8, 22-23; 2^4:19, 27-28. 1919.

Wortley, E. J. The transmission of potato mosaic through the tuber. Science n. s. 42:460-461. 1915.

For such comparison plots of about one-fifth acre each were grown in Aroostook County in 1918. Two plots were planted with seed that came respectively from healthy and mosaic hills of a plot which was planted in 1917 with a good commercial strain of Green Mountains. The former, with 11 per cent of the hills removed during the season because of their showing mosaic symptoms, yielded at the rate of 89 barrels an acre while the latter yielded at the rate of 69 barrels an acre, with no hills removed[8]. A similar pair of plots of a commercial strain of Bliss Triumphs showed yield rates of 75 barrels, for the comparatively healthy plot with 15 per cent of the hills removed, and 53 barrels, for the all-mosaic plot with no hills removed. The differences might have been greater if the plants on the plots had not been frozen down in the latter part of June.

The preceding comparisons refer to healthy and entirely diseased lots and so may seem to be somewhat inapplicable to conditions where a large number of the plants are not diseased and where these may possibly be able to make up for the deficiency of affected plants by making better growth at their expense. However, in 1918 a nearly healthy Green Mountain fifth-acre plot, with 13 per cent of the hills removed, yielded at the rate of 84 barrels an acre, while another plot from the same strain, with 45 per cent of the hills mosaic but with no hills removed, yielded only a half-barrel more per acre. Furthermore, the effect of mosaic upon yield is important because of the natural increase of the disease. In the absence of any control measures it has been found that often a healthy lot of a susceptible variety will show symptoms of the disease in some hills the next year after being grown near to diseased stock and will

[8]The removal of hills from the healthy plot probably was largely a loss. It has been determined (Stewart, F. C. Missing hills in potato fields: their effect upon the yield. N. Y. (Geneva) Agri. Exper. Sta. Bul. 459: 45-69. Fig. 3. 1919.) that on the average the adjoining hills make up in increased yield 46.4 per cent of the loss resulting from a missing hill when such missing hills are due to failures to germinate. It is not believed, however, that this rule is applicable to the plots under discussion since the diseased plants were not removed until the growing season was nearly half over and so previous to that time they were taking their share of space, water and food materials which would have been used for the benefit of the adjoining hills if these diseased hills had been represented by misses from the start.

thereafter from year to year have a larger percentage of hills affected, thus approaching the all-mosaic condition with which the most of the yield comparisons are concerned.

Transmission by the Tubers.

Three questions are involved with tuber transmission—whether diseased stock recovers to any extent, whether such stock becomes worse from season to season, and whether tubers from apparently healthy plants may transmit mosaic through the dormant season.

It appears that when a plant once becomes diseased, there is no recovery by it or by any of its progeny. In 1917 over a hundred mosaic hills were selected. Progeny of theirs, several hundred hills, were grown in 1918 and showed mosaic in all cases. All healthy plants were removed from two one-fifth-acre plots grown in 1917, and in 1918 these two lots, grown again on fifth-acre plots, contained no healthy plants. A number of small lots all-mosaic in 1917 were again entirely diseased in 1918.

These results were duplicated with stocks grown in 1918 and tested in 1919. Over 150 hills were selected, furnishing 1100 hills of progeny, all mosaic. Stocks used previously in the two larger plots and in smaller lots were continued in use but remained diseased.

It is commonly considered that mosaic increases in severity from year to year and certain field observations seem to confirm this idea. In these cases, however, there was a tendency for the disease to change very little in severity as a result of transmission through the tubers from one season to the next. For example, stock selected as showing a medium stage of mosaic might show a slight stage in some hills and a bad stage in others the next season, but the average would be medium. The same was true of stock selected as showing a slight stage or a bad stage.

In this connection it should be pointed out that treatment of seed tubers with formaldehyde, corrosive sublimate, and heat have not appreciably affected the percentage of mosaic[9]. This is not surprising in view of the evidence, presented in this bul-

[9]Orton, W. A. Op. cit.

letin, that the disease is caused by something in the juice of the tuber or plant and not, as in many potato diseases, by an organism upon or in the surface layers of the tubers.

Tubers from apparently healthy plants often have produced mosaic plants. In fact, many groups of healthy plants have been selected but in any such lot of stock the disease has always appeared the next season unless the selected healthy group had been grown under certain conditions, to be described later in this bulletin. The frequency of the appearance of the disease in stock selected as being healthy was at first puzzling and led to tests of the communicability of the disease.

PROOFS OF INFECTIOUSNESS.

GRAFTS.

In order to disclose whether the disease could be transmitted from one plant to another, tests were made with methods that seemed most likely to succeed if such transmission were possible. Grafts were made with plants in the greenhouse, in the field both in the open and under cages, and with tubers in the field.

In preliminary trials in the greenhouse two methods were used, the cleft-graft and the inarch. Both gave cases of transmission, the originally healthy scion becoming mosaic after being grafted upon a diseased stock while its parent remained healthy. The former method proved to be more practical for securing successful grafts. By it the base of the scion was sliced down to a thin wedge, inserted between the parts of the split stock, and held in place with the help of adhesive tape.

The cleft-graft method was used somewhat more extensively in the field the following season, 1917, with 62 per cent of the originally healthy scions becoming diseased. In this test the parents of the scions were not observed.

In 1918 the same method was used again. In only thirty-three grafts of healthy scions on diseased stocks was satisfactory growth obtained and in each of these the scion became mottled while the parent plant remained healthy. In the case of five grafts of diseased scions on healthy stocks, these previously healthy stocks showed mosaic in their later growth. Eleven

controls, each consisting of healthy scion and stock, remained healthy, showing that the operation of grafting was not the cause of mottling.

Since aphids, or plant lice, were very abundant in 1918 and had not been controlled in previous grafting experiments, final tests were made both in the field and in the greenhouse with these insects eliminated[10]. In the greenhouse any vigorous new growth that was made by a healthy part of the graft became mosaic unless both stock and scion were healthy. In the field under cloth insect cages, healthy stocks produced mosaic shoots in spite of the fact that the mosaic scions soon died because of shading. That this was due to the grafting is indicated by the absence of mosaic in the stock at the time of grafting or at any time in ungrafted check stalks in the same hills.

In the preceding experiments either the Bliss Triumph or the Green Mountain variety was used. One test with Irish Cobblers—very resistant to mosaic—was made in 1919 with mosaic scions upon uncaged stocks. The result was that mosaic appeared in the new branches from the grafted stalks while ungrafted stalks remained healthy.

Tuber grafting was attempted in the following manner. A supposedly mosaic tuber and a likewise supposedly healthy tuber were split lengthwise into halves. The freshly cut surfaces of one-half of each were immediately brought into contact and the two halves securely bound together and planted in this condition. The remaining halves of the healthy and diseased tubers were planted separately as checks. In 14 such cases the separately planted or check halves produced diseased and healthy plants in accordance with the supposed condition of the original tubers. Likewise all of the diseased tuber halves in the attempted grafts produced mosaic plants. On the other hand only 11 of the healthy tuber halves in the attempted grafts produced healthy plants while 3 produced mosaic plants. Examination showed that in the case of the 3 last mentioned actual union had been established between the cut surfaces of the healthy and diseased tuber halves. No such union had occurred in the 11 cases where no transmission of the disease occurred.

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[10]This precaution had been made necessary by the results of certain insect experiments which will be described later.

It is clear that these results, secured under different conditions and at various times and places, all indicate that such contact of plant tissue as is possible in a graft enables the causative agent of potato mosaic to pass from a diseased plant, or plant part, to one that is healthy, resulting in the latter becoming affected also.

JUICE INOCULATIONS.

While tests of communicability were being carried on by means of grafts, similar tests with the transference of plant juice were also performed. Both tubers and plants were used. Experiments were made in the greenhouse and field, and three varieties of potatoes were employed.

The juice from the crushed leaves and stems of diseased plants was introduced into a cavity in a half of a split tuber. Sometimes both the treated half and the untreated half, the latter planted as a control, produced mosaic plants. Often both produced healthy plants. Occasionally only one produced a diseased plant and always it was the treated half. Hence it appeared possible to transmit mosaic by inoculating seed tubers with the juice of affected plants.

Several methods were used in 1918 for introducing juice from crushed plants and tubers into the stems and leaves of healthy plants. While no treated plants developed mottling during that season, progeny of some of the groups of plants showed a high percentage of disease the following summer. During the latter season the progeny of check plants, treated the same as the inoculated plants but with water used in place of the juice of a diseased plant, were mosaic in 24 per cent of the hills, probably because of natural transmission in the field in 1918. Progeny of plants whose stems were split and partly immersed for several days in the juice obtained by crushing tubers from mosaic plants, were all mosaic. Of the progeny of plants which in 1918 were inoculated by means of capillary glass tubes inserted into the leaf stalks or petioles immediately after these tubes were taken, filled with juice, from a similar position in diseased plants, 77 per cent were mosaic. Other methods consisting of the application of juice, by means of a brush, upon rubbed, bruised, or slashed leaves, did not prove so effective.

New methods were used in the greenhouse with better results. Juice from crushed mosaic plants was applied to the young leaves of a healthy plant, growing from half of a split tuber, and rubbed in by crushing the leaves somewhat with the fingers. This application was made several times in the course of a month, beginning when the plants were from 2 to 6 inches in height. The plants thus treated usually became mosaic if new growths were produced. The same results were secured at the same time by rubbing and crushing together the leaves of mosaic and healthy plants. All new growth was healthy which was produced by the untreated plants from the check halves of the seed tubers or by control plants treated with juice from healthy plants. All these greenhouse plants were free from plant lice.

The former of these methods was used in the field in 1919, the Irish Cobbler variety being added to those used previously, namely, Bliss Triumph and Green Mountain. Some of the non-inoculated plants became mosaic early, due to infection in 1918[11], and an equal number of the inoculated ones also, from the same tubers. This was true also for some plants treated with the juice of healthy plants. Of the other plants in the experiment, all remained healthy except those inoculated with juice from mosaic plants. Of 48 such plants, 47 became mottled—doing so before aphids became numerous—in a series wherein juice was transferred between plants of the same variety. Forty-three of 47 such plants became mottled in another series wherein juice was transferred either from Bliss Triumph to Green Mountain, from Green Mountain to Bliss Triumph, from Green Mountain to Irish Cobbler, from Irish Cobbler to Green Mountain, or from Irish Cobbler to Bliss Triumph. The plants that were mosaic from 1918 infection did not show mottling until after the inoculations had been begun, so that, in spite of the customary precautions, a chance was offered for accidental transmission whenever healthy juice was applied to a series of plants that included some of these mosaic plants. This did not occur, thus showing that rubbing and bruising the leaves of a healthy plant subsequent to such treatment of a diseased plant was not sufficient

[11]This assumption seems reasonable as a result of various experiments, with plant lice, described later.

for transmission. The absence of symptoms previous to that time was not the reason inasmuch as the virulent juice used for successful inoculations sometimes came from diseased stock that had not yet shown mottling.

Variations of the preceding experimentation were made in other series of inoculations in 1919. Inoculations were made in Green Mountain plants protected by insect cages, with similar results. In the cages, and also in the open both within and between varieties, single inoculations were made for comparison with the usual method of repeating the inoculation several times, with the same results even when made as late as July 20. In four series the juice for inoculation was transferred from plants in the worst stage of the disease, both within each variety and from Mountains to Cobblers, with the resultant appearance of the same sort of symptoms whereas the induced mosaic was often but not always of the worst type in the other inoculations.

Artificial transmission of potato mosaic by means of grafting and juice inoculation thus demonstrated the infectious nature of the disease and made necessary the discovery of a natural means of transmission. This was found to be a certain type of insects, as will be explained in the next section.

INSECTS AS CARRIERS.

EFFECT OF USING INSECT CAGES IN THE FIELD.

Simultaneously with the first experiments with grafts and juice inoculations, preliminary tests were made regarding transmission by insects. Potato plants were grown throughout the season of 1917 under cheesecloth cages. These cages were not entirely insect-proof but their use resulted in a reduction of mosaic that season. Only 5 per cent of the tubers from the healthy caged plants produced mosaic progeny the next season, while other healthy plants, grown outside the cages, produced progeny the following year with much greater percentages of mosaic.

Again in 1918 healthy plants were grown under cages. On account of the poor quality of the cheesecloth obtainable and the abundance of aphids in the field, many of these insects were found on some of the caged plants. However, all the tubers

from the caged hills were found in 1919 to be healthy, while uncaged stock of the same kind, grown near by, was mosaic in 1919 in 35 per cent of the hills for Bliss Triumphs and in 49 per cent for Green Mountains.

These results, wherein the normal spread of mosaic in the field was greatly reduced or eliminated by protecting healthy plants with insect cages, merely support other evidence that insects transmit the disease. Such evidence has required the transfer of insects from mosaic to healthy plants, with check plants both untreated and treated with insects from healthy plants.

PLANT LICE IN THE GREENHOUSE.

Since greenhouse conditions are more favorable to the control of insects, and since Allard[12] had demonstrated the transmission of tobacco mosaic by aphids, experiments with one species of these insects—the pink and green potato aphid, *Macrosiphum solanifolii* Ashmead—were begun in the greenhouse in the winter of 1917-18. Bliss Triumph plants were grown, of which about a fifth appeared mosaic when a few inches tall, as the result of field infection during the preceding summer. Aphids were permitted to disperse from these affected plants and also artificial transfers were made. Within a few weeks half of the plants were mosaic, the additional ones only in the youngest leaves instead of in all the leaves as when following tuber transmission. Moreover, all the progeny of these plants, even of those apparently healthy, were mosaic when grown in the winter of 1918-19. This and other cases of aphid transmission without the appearance of mosaic until the second generation is grown, affords the best explanation for the frequent appearance of mosaic early in the growth of the progeny of plants selected as healthy in a field containing aphids and mosaic plants. The same stock grown in part in the greenhouse in 1917-18 was used for field planting in 1918 when less than a fifth of the hills were mosaic.

A similar experiment with the same variety was performed in the greenhouse in 1918-19. Part of a lot of tubers was kept free from aphids by fumigation and only 11 per cent of the

[12]Allard, H. A. Op. cit.

plants showed mosaic symptoms, from field infection. Another part of the same lot was grown near to a group of mosaic plants, of the same variety, which were heavily infested with aphids. Of this portion of the lot, 17 per cent were mottled from the beginning, from field infection. In addition 50 per cent of the group developed mosaic symptoms following dispersal of the aphids from the mosaic group, the plants next to the mosaic group all doing so.

A lot of 30 Green Mountain tubers in storage produced sprouts which became lightly infested with spinach or common green peach aphids (*Myzus persicae* Sulz.) from a neighboring heavily infested lot of sprouted tubers that had come from a purely mosaic stock and that later produced mosaic plants. Of these 30 tubers, 17 per cent produced plants that were mottled early, from field infection, while in addition 20 per cent showed mottling later, usually in shoots from eyes of the bud end and therefore probably the ones first to become exposed to aphid attack. A much larger part of the same general stock planted in the field was less than 20 per cent mosaic.

Green Mountain plants also were grown under insect cages in the greenhouse during the winter of 1918-19. In one experiment five tubers were split. A half of each produced a check plant which was uncaged and untreated and remained healthy. Of the other five plants, all were caged, two being treated with aphids from healthy potato plants and three with aphids from mosaic potato plants. The transfers of aphids were made at three different times and were followed finally by tobacco fumigation to kill the insects in order to save the plants for later observations. The former two plants remained healthy but the three others became diseased.

In another experiment with the same variety, 12 tubers produced 53 plants which showed no evidence of mosaic when small. Twenty-one of these healthy plants, selected so as to represent each of the original 12 tubers, were kept as untreated controls and remained healthy. About half of these were caged until almost full-grown. Eighteen others likewise representing each of the tubers were fed upon by aphids from mosaic potato plants. The insects were introduced upon diseased leaves which were laid upon the caged healthy plant when it was young, from 3 to 13 inches tall. The aphids were on the average about

130 in number when transferred and were allowed to remain for a week before being killed by tobacco fumigation. The mottling appeared after an average interval of 26 days, upon only the topmost leaves of any shoot. Thirteen or 72 per cent of the 18 plants became mosaic, due to transmission by the aphids. Many precautions were taken to eliminate the possibility of accidental infection, the soil being steam-sterilized, the seed-cutting knife flamed, contact avoided, white flies (*Aleyrodes vaporariorum* Westw.) and any species of aphids other than the one in use entirely eliminated, and conditions kept similar for controls and inoculated plants regarding light, temperature, humidity, location of seed piece in the tuber, soil fertilization and watering. Moreover, with controls other than the untreated ones, aphid-free mosaic-leaves were laid upon the plants when young, or aphids from healthy potato foliage and from radish plants were introduced, all without any effect respecting mosaic.

Since potato mosaic may be acquired by one generation without the symptoms being shown until the tubers produce the second generation of plants, the preceding groups of plants were dug and the tubers planted in the field in 1919. The tubers from mosaic shoots produced diseased plants. Even those from apparently healthy shoots fed upon by aphids from diseased plants also produced mosaic plants. Those from the 35 other healthy plants produced healthy plants except the ones from two plants. Upon these two a few aphids were found which were of unknown origin, possibly from diseased plants.

In a third experiment, 9 Green Mountain tubers produced healthy plants, six seed pieces being cut from each tuber. The six plants from each tuber were put into as many separate groups having different treatments with results as follows. Two groups of untreated plants, one caged and the other uncaged, remained healthy. In the third group, caged, wingless spinach aphids were introduced on leaves which were impaled upon a stick thrust into the soil so that the aphids, about 170 in number, had to traverse the stick and soil to reach each caged plant, and 89 per cent became mosaic. In the fourth group, caged, the aphids, about 130 in number, were introduced to each plant on a piece of gauze, and 22 per cent became mosaic. In the fifth group, caged, 20 winged aphids were introduced into each cage in a small bottle and 11 per cent became mosaic. In the

last group, uncaged, each plant was kept in contact with a mosaic plant grown in a separate pot and one became mosaic following the detection of the presence of escaped aphids.

A final experiment yielded the best results because disease-free stock was used and the plants were grown during the spring and summer, thus being exposed to such conditions of light and heat as to enable them to maintain active growth for a longer period than the plants grown previously. Ten tubers were each split into four parts; two parts produced plants which were left uncaged and untreated, as checks, and two produced plants that were caged until after aphids had been introduced, allowed to feed, and killed by fumigation. The aphids, of the spinach kind, were taken from mosaic plants, about 150 in each case. To fifteen plants they were introduced by the leaf-on-stick method, described above, and all these fifteen plants became mottled within a few weeks. To five plants they were introduced, when on the terminal vegetative buds of mosaic shoots, within an open bottle laid upon the soil. This was an unfortunate method since many of the aphids soon became injured or killed by coming into contact with moisture collecting on the inside of the bottle, so that only one of the five plants became mottled. The 20 check plants remained healthy except one which became slightly mottled—the last one to do so—after uncontrolled aphids had been found on it several times.

The greenhouse experiments that have been described showed that both spinach aphids and potato aphids—two species of plant lice commonly found upon potato plants in Maine[13]—can transmit potato mosaic from diseased to healthy plants, and that this transmission sometimes may not be followed by the development of mosaic symptoms until the tubers produce the second generation of plants. Since plant lice in northern Maine become noticeable or numerous only during the latter part of the season, it is made clear how mosaic may commonly be spread in the field without the effects being apparent until the next season.

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[13]Patch, Edith M. The potato plant louse. Me. Agric. Exper. Sta. Bul. 147:235-257. Figs. 25-33. 1907.

Patch, Edith M. Pink and green aphid of potato. Me. Agric. Exper. Sta. Bul. 242:205-223. Figs. 47-49. 1915.

Also oral information has been received from the same authority concerning spinach aphids.

PLANT LICE IN THE FIELD.

The positive results of the greenhouse experiments were confirmed in the field in 1919. Eight Green Mountain tubers from a mosaic-free stock were each divided into three parts, a tuber furnishing the plants for each cage. In four cages the plants were fed upon by spinach aphids which were introduced from radish plants and they all remained healthy. In the other four cages the plants were fed upon by aphids introduced from mosaic potato plants and mosaic symptoms appeared in three of the cages before the plants were harvested. Nine similar tubers were split, a half from each being planted in the open where it produced a healthy plant. The other halves were planted in three cages into which spinach aphids from mosaic potatoes were introduced. Three of these nine plants became mosaic The smaller percentage of infected plants in these field-cage experiments, as compared with those in some of the greenhouse experiments, is probably due to the much greater size of the plants in relation to each hundred aphids used, the 1919 season being very unfavorable to the development of aphids and favorable to the rapid, early growth of potato plants.

The various proofs of aphid transmission furnish the best explanation for certain field observations that have been made. In 1918 aphids were unusually numerous in northern Maine, much more so than in 1917. If they are an important cause of the spreading of mosaic, such spread should be greater in 1918, other conditions being equal, than in 1917. In fact it was greater, judging from certain stocks, grown in fifth-acre plots, that had all mosaic plants rogued out both in 1917 and 1918. These showed mosaic in 1918 in from 11 to 16 per cent of the hills as the result of infection from near-by diseased plots in 1917, while they showed mosaic in 1919 in from 20 to 30 per cent of the hills as the result of such infection in 1918. This difference is made more striking by the fact that these stocks were grown each next to all-mosaic plots in 1917, but in 1918 were grown each next mosaic-free or half-mosaic stock. In 1918 one rogued stock was grown next a half-mosaic stock while two rogued stocks were grown nine and eighteen rows away, respectively. The former showed mosaic in 30 per cent of the hills in 1919 and each of the latter in only 20 per cent. It is thus seen that

crease in the seasonal abundance of aphids and by greater proximity to diseased stocks, and therefore by conditions that seem the spread of mosaic was increased apparently both by an into favor aphid dispersal from diseased to healthy plots.

During 1918, the season of great abundance of aphids, three lots of tubers were harvested at progressively later dates during the increase in numbers of the plant lice. From each of 78 healthy hills—mostly Green Mountain—growing near to mosaic hills, one tuber was removed on August 15 and another on August 26, the remainder being harvested on September 12. Meanwhile aphids, which became noticeable on potato plants the latter half of July, had become very numerous about the middle of August and were more excessively abundant as the end of the month was approached, seeming when migrating to be as abundant as the flakes in an ordinary snowstorm. The three sets of tubers in 1919 produced plants mosaic in 6, 14, and 50 per cent respectively. Apparently some of the transmission occurred before August 15 but most of it took place after August 26. Such late infection of the tubers is apparently due to the late development of the chief cause of the spread of mosaic, namely, abundant dispersing aphids.

FLEA BEETLES.

Five caged groups of healthy Green Mountain hills were fed upon by flea beetles *(Epitrix cucumeris* Harris)[14] for a week, several hundred from all-mosaic potato plants being introduced into each cage. As controls, four similar groups were treated likewise except that the beetles were taken from plots of mostly healthy potatoes or from bushes. All the plants in this experiment remained healthy until harvested. This result at least indicates that flea beetles are not important in spreading potato mosaic, since the artificial infestation was much more severe than any ordinary natural one while the contemporary artificial infestations with aphids, described as causing mosaic transmission, were not as heavy as natural ones.

[14]This insect is the subject of Bulletin 211 of the Maine Agricultural Experiment Station.

COLORADO POTATO BEETLES.

A similar test was made with larvae of Colorado potato beetles (*Leptinotarsa decemlineata* Say.), commonly called potato bugs. A hundred or more actively growing individuals were transferred from mosaic plants immediately to each of 10 healthy plants where they did more damage than is usually permitted by potato growers. However, the plants remained free from mosaic until dug. Checks, consisting of 5 untreated plants in the same cages as the 10 treated ones and of 9 plants grown in 3 other cages and fed similarly with beetles from nearly mosaic-free potato plots, also remained healthy.

OTHER INSECTS.

It is quite probable that sucking insects other than aphids contribute to the spread of mosaic. Such insects, including leaf hoppers and plant bugs, feed upon potato plants. A beet disease apparently somewhat similar to potato mosaic is transmitted by beet leaf hoppers (*Eutettix tenella* Baker)[15]. Aphids often appear to be more abundant than other types of sucking insects, but are smaller individuals than some types and may be less prevalent in some places and seasons. However, all seem to require similar control measures, regarding mosaic or otherwise, although much study could be done profitably upon the relations between mosaic and the various potato insects.

Other Possible Factors in the Spread of Mosaic.

THE SEED-CUTTING KNIFE.

The same knife was used, in 1919, to cut a mixture of mosaic and healthy stocks of tubers, to test whether the knife would carry enough juice from a diseased tuber to a healthy one to transmit the disease. First a tuber from an all-mosaic stock was cut, then one from a rogued stock, and so on. Each

[15]Ball, E. D. The beet leafhopper and the curly-leaf disease that it transmits. Utah Agri. Exper. Sta. Bul. 155. 56 p. 5 figs. 5 pl. 1917.

Shaw, H. B. The curly-top of beets U. S. Dept Agri. Bur. Plant Indus. Bul. 181. 46 p. 9 figs. 9 pl. 1910.

tuber—200 in all—was cut into four pieces, those from all-mosaic stock being sliced across and those from the rogued stock being quartered. The cut seed was further mixed in a sack and left for over a day. Then the seed pieces from the all-mosaic stock, having been cut in a different shape from those of the other stock, were sorted out and discarded. The row of 400 plants grown from the rest contained 72 mosaic plants. These evidently were diseased because of infection in 1918, since another check row of 400 plants, from 100 tubers of the same barrel, contained 85 mosaic hills although no chance had been given since harvesting in 1918 to get the disease.

A similar test, but involving contact of vines in the row also, was made with the same stocks. Instead of removing the seed pieces of the all-mosaic stock, all the seed pieces were planted unsorted in two rows. Of the 800 plants 475 were mosaic, 400 of course coming from the all-mosaic stock. Since the additional 75 is less than the 85 in the check row, no transmission since the harvesting of 1918 was evident, except of course that through diseased tubers.

In 1918 a number of tuber units, each a group of hills from one tuber, were partly mosaic. It was thought that such partial infection of tuber units might be due to knife transmission. Consequently in 1919, when most of the tuber units were planted, usually three knives were used in rotation, each one being immersed in a sterilizing solution, 4-per cent formaldehyde, when not in use. However, the partial infection of tuber units was as common as in 1918 and as in the case of the tuber units planted in 1919 without knife sterilization.

These various tests indicate that the seed-cutting knife is negligible as a factor of mosaic transmission.

CONTACT.

The effect of contact between mosaic and healthy plants was first studied in the greenhouse. As has been described, of nine healthy plants each grown with stems and leaves in contact with those of a mosaic plant, one showed mottling but not until after a few uncontrolled aphids, possibly from mosaic plants, were discovered upon it. At about the same time 8 healthy plants from as many different Green Mountain tubers were

grown in the same pots with mosaic plants, roots as well as stems and leaves being intermingled. Opportunity for infection through the roots was increased by the transplanting of the healthy plant into the potful of soil containing the diseased plant, with more or less consequent breakage of roots. The 8 plants remained healthy, as did 16 others grown from the same tubers and by themselves. This result was in marked contrast with a contemporary experiment, already described, wherein a certain method of transferring plant lice resulted in 100 per cent infection.

In the field, 18 healthy Green Mountain plants were grown under cages together with mosaic plants. Six soon crowded out their diseased companions by shading them. All remained healthy except for the uppermost leaves of one stalk of one plant. These were mottled on August 27, had aphid skins and aphids clinging to them, and were near a small hole punched accidentally in the cloth.

In one of the tests with the seed-cutting knife, as described above, a mixing of mosaic stock in the rows with rogued stock did not result in any increase of mosaic over that seen in the same rogued stock unmixed.

In 1917 five Green Mountain hills were selected as being healthy and were harvested. In 1918 the hill lots from these five hills were found to be partly mosaic, often with several healthy hills between successive mosaic ones in the row. The healthy hills were harvested separately and classified according to the proximity to mosaic hills. Class 1 consisted of hills each between two mosaic hills, class 2 of hills each between a mosaic and a healthy hill, and classes 3, 4, 5, 6, and 7 respectively of hills each with 1, 2, 3, 4 and 5 healthy hills between it and the nearest diseased hill. The next season the tubers, 337 in all, were planted uncut. For class 1 the mosaic percentage was 54 per cent, for class 2, 63 per cent, and for the other 5 together, 40 per cent. For classes 3 to 7 the percentage was respectively 56, 24, 54, 24, and 17 per cent. Being next to a mosaic plant in the same row thus seemed to increase the chance of infection as much as 54 or 63 per cent is greater than 40 per cent. It probably is a contributing factor in mosaic transmission only or chiefly by aiding aphid transmission.

Similar evidence was secured by comparing two treatments of Green Mountain lots. Removal of both the mosaic hills and

all the healthy hills next to mosaic hills in the row did not cause any reduction of infection as compared with the removal of only the mosaic hills.

It seems from the facts so far secured that contact infection can not be very common or important, especially when considering the results obtained from artificial inoculations and with aphids. However, some infection by contact possibly may occur too late to be evident during the season in which it occurs. Experiments on this point are not completed but stocks are available for growing the second generation in 1920 to test this possibility. Of course any measures necessary to prevent contact would be included in those necessary to avoid aphid transmission, which obviously often is made easier by contact although apparently frequent without contact.

SOIL.

The causes of many potato diseases are carried both from place to place and from season to season by means of soil. It is maintained that 80 per cent of field infections of tobacco mosaic originate in contaminated soil[16]. Hence it has seemed necessary to disclose any soil harboring of potato mosaic that may occur.

In the greenhouse twelve Green Mountain tubers were split. Half of each was planted in steam-sterilized soil and the other half in soil from which a full-grown mosaic plant had been removed either a day or a fortnight previously. The 24 plants were all healthy, as was also the second generation of the same stock.

While soil transmission was favored in this greenhouse test by the shortness of time between the growth of succeeding crops in the same soil, there were lacking certain factors in the possible soil-harboring in fields, namely, old stalks, volunteer potato plants, and hibernating insects. Therefore three rows of Green Mountain rogued stock were planted in 1919 across the sites of a 1918 twenty-per cent mosaic plot and a wholly diseased one, both of Green Mountains. All mosaic hills were dug and the seed pieces examined to determine the volunteers. Disregarding

[16]Chapman, G. H. Op. cit. See p. 80.

the latter, 28 per cent of the hills upon each site showed mosaic, mostly early, from infection in 1918.

Similar negative results were given by a more extensive test wherein 19 rows of rogued stock were planted across the sites of fourteen of the 1918 plots. Practically all the mosaic which occurred was shown by July 30 and so was judged to be due to infection occurring in 1918. Mosaic hills were dug and, disregarding volunteers, formed 23 per cent of the total, 4,466. A record was kept for each of the 14 parts. Among these there were only four marked variations from the average. These consisted of a deviation upward and one downward for the sites of two half-mosaic plots and similar deviations for the sites of two comparatively mosaic-free plots.

It therefore appears that the cause of potato mosaic is not transmitted in soil, except in discarded or ungathered tubers. These, however, may constitute an important means for the harboring of mosaic from season to season in a piece of land, since they produce volunteer plants, which, if mosaic, furnish a number of well-distributed sources of infection through aphid transmission.

LOCALITY.

The symptoms of mosaic may vary according to the region. The same stock of mosaic potatoes has been divided, part being sent to Colorado and part kept in northern Maine. The usual mottling of mosaic stocks was seen in Maine but did not appear in Colorado. With part of a stock sent to Washington, D. C., some mottling was noted but there were a number of doubtful cases, while the part kept in Maine was distinctly mottled.

When a number of lots were divided and planted at the two farms of the Maine Agricultural Experiment Station, the part of a lot grown at Highmoor Farm in the southwestern portion of the state often showed much less mottling than the part grown at Aroostook Farm in the northeastern portion. In two out of three seasons the difference has been very marked and the reverse was never seen.

Such a difference is not due to recovery in one place but rather to an obscuring of the mottling, as indicated by the reappearance of distinct mottling in affected stock returned to north-

eastern Maine. Also, in the latter region hot weather sometimes has been observed as apparently causing mosaic plants to lose their mottling, which again was plain after the return of cool weather.

The effect of differences in locality upon the symptoms shown by plants already diseased of course has no real effect upon the spread of mosaic. Undoubtedly one condition alone—the abundance of aphids, if no other—may vary enough in different regions or localities to affect the spread of the disease. Such problems are yet to be worked out.

VARIETAL RESISTANCE AND IMMUNITY.

The Irish Cobbler variety is practically free from mosaic in northern Maine, in marked contrast to the Green Mountains and Bliss Triumphs. Other varieties resemble the Cobblers. The extent and possible causes of immunity and resistance among the varieties are being determined.

FERTILIZER VARIATION.

Variations in the constitution of commercial fertilizers and the addition of special substances to the soil have not had any great or important effect upon mosaic already acquired. How much they might influence the resistance of susceptible varieties to mosaic infection, is being studied.

SPRAY METHODS.

Direct effect of any kind of spray upon mosaic has not been evident and could hardly be expected in view of the difference between the location of the spray on the outside of the leaves and that of the infectious substance in the juice. However, certain spraying methods may help to affect the mosaic problem through the control of plant lice.

METHODS OF CONTROL.

HILL SELECTION.

For several years many groups of healthy hills, numbering many hundreds of plants altogether, have been selected in the

experimental plots in which diseased plants, too, were growing. With the exception of those protected from insects, as previously described, no such lot of potatoes was free from mosaic in the next generation after selection. When selected in 1918, the various lots in one 1919 series contained from 12 to 76 per cent of mosaic. Altogether there were about 4,000 hills of which 1,200, or 30 per cent, were mosaic. This is not surprising since the selected hills were grown near to mosaic hills and it is probable, judging from experiments discussed previously, that aphid transmission occurred too late in the season of 1918 for symptoms to appear and was followed by the usual tuber transmission.

The selection of healthy hills, then, does not result in a mosaic-free stock when aphids are uncontrolled. Further selection among 140 healthy hill lots—mostly Green Mountain and a few Bliss Triumph—was made on the basis of the number of tubers, whcih varied from 2 to 12 in a hill. A high percentage of mosaic, 86 and 60 per cent respectively, was shown by the progeny of hills with 2 or 3 tubers in a hill. Otherwise the mosaic percentage, varying from 30 to 53 per cent, showed no consistent relation to the number of tubers. It thus seems that possibly the increase of mosaic could be reduced somewhat by discarding hills with the lowest yields but it would not be avoided by this practice, and such hills are discarded because of the smallness of their yield whenever hill selection is practiced.

SELECTION OF TUBERS.

Frequently the tubers from a healthy hill vary in regard to mosaic, some being healthy and others diseased. To determine whether the selection of tubers according to size would have any effect upon mosaic percentage, each of the 140 hill lots which were considered in the preceding section was planted in the order of decreasing apparent size of the tubers. Later observations showed that half of them contained both healthy and diseased tubers, the latter tending to be more numerous as the relative size of the tubers was greater. The tendency, however, was not marked enough to make it seem desirable to select tubers according to weight or size. The same conclusions resulted from a similar study of 98 partly diseased hill lots of which the 2 to 6 largest tubers of each were planted.

In 1918, stock unrogued and partly mosaic in 1917 was divided into two parts, one unsorted and the other with tubers of 2 ounces and less in weight discarded. The percentage of mosaic differed only two-thirds of one per cent, being about 45 per cent for each. The plots observed covered about one-fifth acre each.

SELECTION OF SEED PIECES.

Tuber units, or groups of plants each from a single tuber, are often mixed regarding mosaic, that is, partly diseased and partly healthy. In experiments conducted in 1918 and 1919 with such tuber units, there was a preponderance of mosaic in bud-end hills. This, however, is of no value regarding the problem of control because of the small percentage of tubers that will produce both healthy and diseased plants. It is far more important to take measures which will eliminate all tubers that are either partly or wholly mosaic.

REMOVAL OF DISEASED PLANTS.

Since the selection of hills, tubers, or seed pieces seems, with our present knowledge, to be of no great value in securing or maintaining healthy potato stocks, contrary to experience with certain other potato diseases[17], the results secured by removing diseased hills from seed plots are of interest. This method includes several careful inspections for mosaic plants, their removal as soon as found, and of course harvesting and storing the crop separately from all diseased stock. If only one inspection is made it should not be made until all of the plants from diseased tubers have become large enough to show mosaic. In 1919 in all-mosaic stocks only 67 per cent were mottled in Green Mountains and 89 per cent in Bliss Triumphs by July 9. In the early part of that season the unusually high temperatures probably retarded the development of mottling directly and on the other hand hastened it indirectly by accelerating the development of the plants. All plants in these lots were plainly mosaic by the last of July. A single inspection made late enough to

[17]See Me. Agri. Exper. Sta. Miscel. Publ. 535, on "How to Control Potato Enemies."

get all the diseased plants may leave them in the field long enough to serve as centers of infection if aphids appear early and increase rapidly. Therefore two or more inspections are preferable, so that diseased plants may be removed or "rogued" soon after they show that they are diseased.

In 1917 three one-fifth-acre plots, each consisting of 6 rows next to an all-mosaic plot, had from 32 to 49 per cent of the hills mosaic. Two—a Green Mountain and a Bliss Triumph—were rogued three times and in 1918 the stocks were mosaic in 11 and 16 per cent of the hills respectively. The third lot, Green Mountain, was rogued once and in 1918 was mosaic in 13 per cent of the hills. Thus roguing in 1917 made a considerable reduction in the mosaic percentage in spite of the proximity to all-diseased plots—no plant being more than a few rows away—and of the abundance of mosaic hills in the lots. In 1918, the year of excessive abundance of aphids, these three lots of stock were planted together, one lot only being next to a half-mosaic plot, and of course they contained fewer mosaic hills. Roguing in that year was not so effective, since the mosaic percentage increased to from 20 to 30 per cent shown in 1919. This is undoubtedly due to aphid dispersal and indicates the need of isolating the seed plot.

ISOLATION OF SEED STOCK.

If healthy stock of a susceptible variety is grown near to mosaic stock it will acquire more or less of the disease. On the other hand, if it is grown so far from mosaic stock that no insects, especially aphids, will come to it except from weeds or healthy potatoes, it may be expected to remain healthy, judging from the evidence at hand. Tests of this method are under way. As far as is known, such an isolated seed plot, even if partly mosaic, may produce healthy potatoes if it is rogued completely of mosaic hills early enough.

RECOMMENDATIONS FOR THE CONTROL OF POTATO MOSAIC.

Do not expect to control or reduce potato mosaic by means of sprays, seed treatment, or soil treatment, except by spraying methods which control plant lice. Use as healthy stock as can

be obtained. Plant at least part of it in a seed plot of sufficient size to furnish seed for the next year's planting. Select land for this purpose as remote from all other potato fields as possible and land which has not grown potatoes for one or more years. Give the seed plot special care. Rogue all mosaic plants from the seed plot as soon as they show the disease. In case aphids are unusually abundant, the spreading of mosaic by them possibly would be reduced by controlling them with suitable spraying methods, which are advised for the seed plot every year inasmuch as even a small and inconspicuous number of aphids may spread mosaic. Such spraying methods, according to recent publications upon this question[18], require adding ¾ pint of "Black Leaf 40" or of a similar nicotine preparation to each 50 gallons of bordeaux mixture. In localities where it is feasible to make a separate spray for aphids, the ¾ pint of nicotine solution is more effective if added to 50 gallons of water containing 2 pounds of laundry soap first dissolved in hot water. Moreover, if preferred, kerosene emulsion may be used instead of the nicotine spray. Regardless of whatever spray is used for plant lice, it is essential that it be applied in such a manner that it reaches the insects themselves, since the effectiveness of the spray depends upon contact. Hence it is necessary to have the nozzles arranged on the spray boom so as to cover the under sides of the leaves and the stalks of the plants, as well as the upper leaf surfaces, with the spray materials. Finally, avoid any chance of mixing the seed-plot stock with the rest by harvesting and storing it separately from the general stock. Repeat this each year.

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[18]Britton, W. E. Eighteenth report of the state entomologist of Connecticut for the year 1918. Connecticut Agri. Exper. Sta. Bul. 211:249-352. Figs. 7-13. Pl. 21-36. 1919.

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